3-2010

Microbiology of Seamounts Common Patterns Observed in Community Structure

David Emerson

Craig L. Moyer
Western Washington University, craig.moyer@wwu.edu

MICROBIOLOGY OF SEAMOUNTS

Common Patterns Observed in Community Structure

BY DAVID EMERSON AND CRAIG L. MOYER

ABSTRACT. Much interest has been generated by the discoveries of biodiversity associated with seamounts. The volcanically active portion of these undersea mountains hosts a remarkably diverse range of unusual microbial habitats, from black smokers rich in sulfur to cooler, diffuse, iron-rich hydrothermal vents. As such, seamounts potentially represent hotspots of microbial diversity, yet our understanding of the microbiology of seamounts is still in its infancy. Here, we discuss recent work on the detection of seamount microbial communities and the observation that specific community groups may be indicative of specific geochemical scenarios, such as iron and sulfur cycling. These observations are based on the metabolisms predicted by phylogenetic characteristics exhibited by the dominant populations found within these microbial communities as compared to the closest related isolate found in culture. Therefore, these studies combine the use of both cultivation-dependent and -independent analyses. Cultivation-independent studies were primarily completed using cloning and sequencing techniques targeting small subunit ribosomal gene (SSU rDNA) biomarkers along with similar biomolecular tools like terminal-restriction fragment length polymorphism (T-RFLP) and quantitative polymerase chain reaction (Q-PCR), which allow for the determination of phylotypes (analogous to species). We discuss the notion of Zetaproteobacteria and/or Epsilonproteobacteria being the most common members of hydrothermal habitats associated with seamounts exhibiting volcanic activity. Another noneruptive seamount scenario is also examined, for example, South Chamorro Seamount, an active forearc serpentinite mud volcano.

INTRODUCTION

Microbial life is remarkable for its resilience to extremes of temperature, pH, and pressure, as well its ability to persist and thrive using an amazing number of organic or inorganic food sources. Nowhere are these traits more evident than in the deep ocean. Much of the deep seafloor consists of cold, relatively static sedimentary environments where heterotrophic microbes exist in significant numbers, but conditions remain relatively unchanged over long periods of time. Mid-ocean ridges associated with diverging plate boundaries are often sites of high-temperature hydrothermal venting and host many chemoautotrophic microbes; however, these systems are more homogeneous with respect to their physical and chemical properties than vent systems associated with volcanic arcs and backarcs (Takai et al.,

2006), for example, seamounts. The enhanced heterogeneity of seamount-hosted hydrothermal systems represents a dynamic range of habitats, providing for the growth of a remarkable diversity of microbes.

First and foremost, underwater volcanoes create seamounts, and the intense volcanism at actively growing seamounts results in a variety of hydrothermal vent environments. Although these settings account for only a small fraction of all seamounts, the hydrothermal venting offers the potential to fuel novel life forms. Older seamounts that exhibit reduced volcanism, or are dormant, may still be conduits for fluid exchange between the rock mantle subsurface and the ocean (Wheat et al., 2004). These fluids may also feed both deep subsurface and/or benthic (bottom-dwelling) microbial communities (Cowen et al., 2003; Huber et al., 2006). Finally, even dormant seamounts that rise to appreciable depths above the ocean floor (i.e., > 1000 m) can impact ocean currents and mixing, potentially resulting in stimulation of microbial communities that feed off the enriched nutrients (see Lavelle and Mohn, 2010). This latter possibility applies to active seamounts as well.

There are estimated to be over 100,000 seamounts that reach a kilometer or more above the seafloor (see Wessel et al., 2010). This large number illustrates the potential scope of seamounts to provide and impact habitats for marine microbes. The majority of seamounts are associated with tectonic processes taking place in Earth's crust, for example, island arcs that have chains of undersea mountains that result from converging plates. Another source of seamounts is undersea volcanism driven by hotspots or mantle plumes within Earth's crust (see Staudigel and Clague, 2010). The Hawaiian Islands in the Pacific Ocean and the Azores in the Atlantic Ocean are spectacular examples of hotspots. Because our knowledge about the role of seamounts as biogeochemical foci for microbial activity is in its infancy, it is instructive to consider another seamount-associated microbial habitat that derives from fundamentally different geological processes.

The importance of hydrothermal vents associated with deep ocean crustal spreading centers as havens for microbial activity has fundamentally changed how we view life on Earth, and enlightened our thinking about other places in our solar system where life might also exist. The iconic features of these sites are black smokers billowing superheated water charged with iron sulfide minerals, as well as dense communities of macrofauna largely fueled by symbiotic relationships with bacteria that provide energy for their hosts using sulfide-rich waters emanating from the vents. The discovery of these deep-sea ecosystems has reshaped our thinking and research agenda regarding extreme oases of life in the deep sea. Some of the most notable findings from over three decades of research on hydrothermal vents are the extension of the thermal limit for life (Takai et al., 2008) as well as the discovery of a host of bacteria and archaea with novel anaerobic and aerobic metabolisms that take advantage of unique suites of energy sources (both autotrophic and heterotrophic) derived from the combination of geochemistry, temperature, and pressure at these sites (Karl, 1995; Nakagawa and Takai, 2008).

Another emerging aspect of microbiology relevant to seamount studies is the capacity for microbes to live in the deep subsurface. The organic and inorganic chemical reactions, as we as the geological processes associated with microbial populations in the deep subsurface biosphere, are interlinked, b little is known of the complexity of thos linkages (Gold, 1992; Whitman et al., 1998). Furthermore, we are only beginning to realize both the phylogenetic diversity of microbes, and the extent of their metabolic activities in these deep biosphere ecosystems. Drilling projects done in deep mines on land have revealed surprising microbial communities living kilometers below the surface and taking advantage of energy sources derived from interactions of water with basement rock minerals (White et al., 1998; Chivian et al., 2008). In the ocean deep-sea drilling into old sediments has revealed bacteria and archaea living up to hundreds of meters below the seafloor (Parkes et al., 2000; Jørgensen and Boetius, 2007). The extent of microorganisms living in oceanic crust is less well understood because drilling into and recovering good samples from hard fractured rock is much more challengin than from ocean sediments. Here, seamounts constitute an opportunity for future studies. First, they represent extensions of Earth's crust above the seafloor, in essence making basement rocks more available for sampling. Second, seamounts may act as permeable conduits for exchange of fluids between the ocean and oceanic crust (see Fisher and Wheat, 2010). Could it be that seamounts represent a new frontier for making discoveries about the diversity and abundance of microbi life in the ocean?

SIZING UP SEAMOUNT MICROBIOLOGY WITH A MICROBIAL TOUR OF SEAMOUNTS

Seawater circulation through the oceanic crust aided by seamount-supported permeable pathways is conducive to microbiological activity because of the large amounts of nutrient-rich fluids that flow through these relatively small volumes of permeable crust (Edwards et al., 2005; Staudigel et al., 2008). Microbial biofilms may develop on fresh basalts, or dense microbial mats (sometimes a meter or more thick) may form in close proximity to active hydrothermal venting at young seamounts (Emerson and Moyer, 2002; Edwards et al., 2005; Templeton et al., 2009). Thus, active submarine-arc volcanoes typify hydrothermal systems that provide abundant nutrient-rich fluids on which microbial communities can live and grow (Figure 1). However, surprisingly little is known about the microbiology of seamounts, especially in terms of community structure and diversity. We compiled a summary of much of the work that has been published to date using culture-independent microbial investigations, and found only 19 papers that have focused on 24 seamounts (Table 1). By comparison, there have been hundreds of papers investigating the different aspects of the microbiology of seafloor spreading centers. Nonetheless, this work illustrates the diversity of habitats that may exist at seamounts, which, in turn, illustrates the variety of geochemical and hydrological conditions that make many seamounts unique. It is too early to make any definitive statements about the types of microbial communities that might be found at seamounts, especially given the incredible diversity of seamount ecosystems. Nonetheless, some patterns with respect to the distribution of

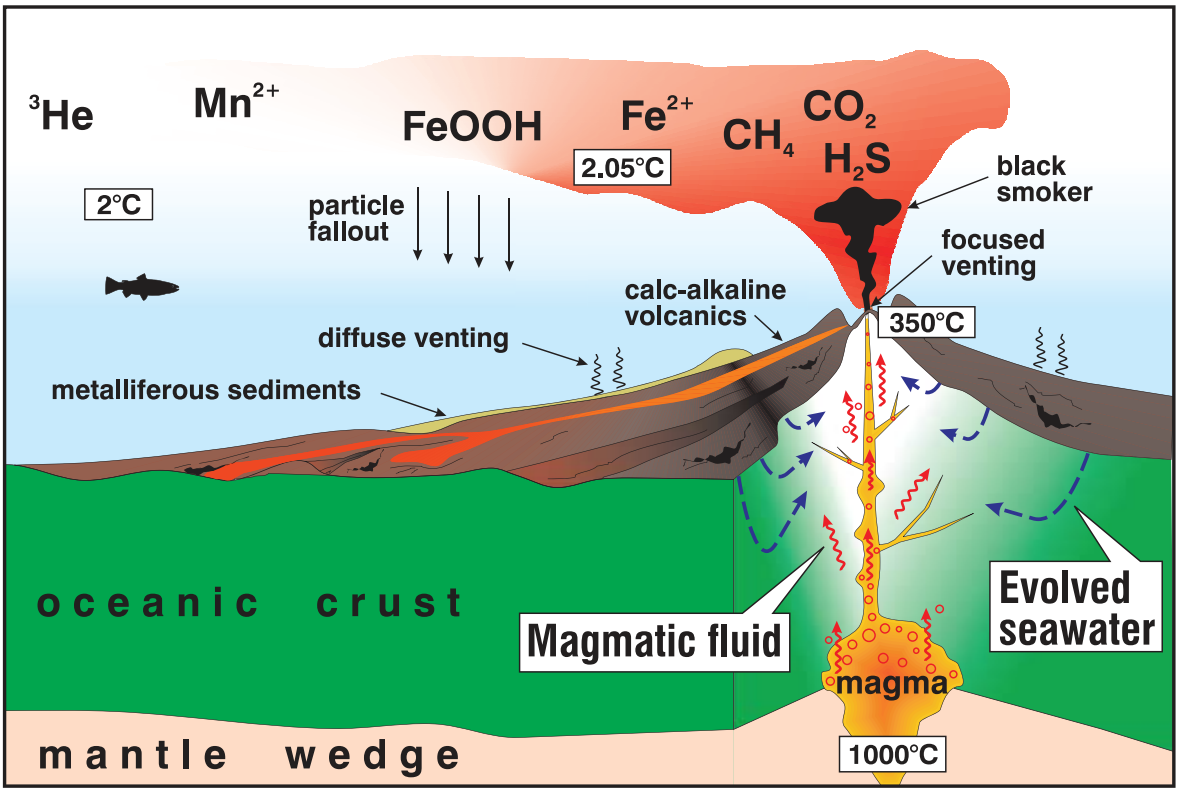

Figure 1. Cross section of a typical submarine arc volcano with an active hydrothermal system. As magma ascends, water and gases contained in magma exsolve and enter the deep hydrothermal system as pressure is released. Cold seawater (blue arrows) permeates the volcano and becomes heated by the hot rock near the magma body. Hybrid hydrothermal fluids (red arrows), derived from seawater and magmatic gas and fluid, buoyantly rise to the summit while altering the volcanic rock (white = alteration). Fluids discharged at the seafloor rise tens to hundreds of meters before they spread laterally in a hydrothermal plume. Local currents disperse the plume, which carries various dissolved and particulate chemical species derived from the magma and the volcanic rock. *Courtesy of Cornel de Ronde, GNS Science*

microbes that thrive at seamounts are emerging. We take a brief tour of the seamounts that have been studied, all in the Pacific Ocean, to illustrate the diversity of habitats that exist and the diversity of microbes that live in those habitats (Figure 2).

Lō`ihi Seamount

Lō`ihi is a seismically active submarine hotspot volcano and the youngest seamount in the Hawaiian Island chain; it is located 35 km southeast of the big island of Hawai`i with its summit rising nearly 4 km above the seafloor (see Spotlight 3 on page 72 of this issue [Staudigel et al., 2010]). Karl et al. (1988) made the first discovery of seamount-associated, Fe-rich microbial mats, showing bacteria with a dominant sheathlike morphology occurring near the summit at Pele's Vents. An eruption at Lō`ihi in 1996 led to the destruction of Pele's Vents and the formation of Pele's Pit, a 300-m-deep pit crater with multiple actively venting sites (Duennebier et al., 1997). The formation of luxuriant Fe-rich microbial mats, along with the conspicuous absence of large benthic macrofauna, is most likely due to the relatively high concentrations of dissolved CO_2 (300 mM) and enriched levels of ferrous iron (50 to 750 µM) in the vent effluent (Wheat et al., 2000). In addition, the summit (presently at a depth of 956 m) is in the oxygen minimum zone, so seawater O_2 concentrations are only 10–15% of saturated seawater (Glazer and Rouxel, 2009).

The initial microbiology study

David Emerson *(demerson@bigelow.org) is Senior Research Scientist, Bigelow Laboratory for Ocean Sciences, West Boothbay Harbor, ME, USA.*
Craig L. Moyer *is Professor, Biology Department, Western Washington University, Bellingham, WA, USA.*

Table 1. Seamount culture-independent microbial investigations into in situ community structure and diversity

Seamount(s)	Geological Setting	Location	Dominant Microbiology/ Predicted Physiology Type‡	References
Lō`ihi	Hotspot	Near Hawai`i, Central North Pacific	Zetaproteobacteria/FeOB Epsilonproteobacteria/HSOB	Rassa et al., 2009 Emerson and Moyer, 2002 Moyer et al., 1995*
Axial	Hotspot	Juan de Fuca Ridge, Northeast Pacific	Epsilonproteobacteria/HSOB Zetaproteobacteria/FeOB	Huber et al., 2003 Kennedy et al., 2003
Vailulu'u	Hotspot	Near Samoa, Central South Pacific	Epsilonproteobacteria/HSOB Zetaproteobacteria/FeOB (detected)	Sudek et al., 2009 Staudigel et al., 2006
Suiyo	Island Arc	Izu-Bonin Arc, Northwest Pacific	Epsilonproteobacteria/HSOB Gammaproteobacteria/SOB	Kato et al., 2009 Higashi et al., 2004 Sunamura et al., 2004
Mariana Arc	Island Arc	Mariana Arc, Western Pacific	Zetaproteobacteria/FeOB Epsilonproteobacteria/HSOB	Davis and Moyer, 2008 Nakagawa et al., 2006
Tonga Arc	Island Arc	Near Tonga, Southwest Pacific	Zetaproteobacteria/ FeOB	Forget et al., in press Langley et al., 2009
Kermadec Arc	Island Arc	Near New Zealand, Southwest Pacific	Epsilonproteobacteria/HSOB Gammaproteobacteria/SOB Deltaproteobacteria/SRB Zetaproteobacteria/FeOB (detected)	Hodges and Olsen, 2009 Takai, et al., 2009 Stott et al., 2008
South Chamorro and Mariana Forearc	Serpentine Muds (ultramafic)	Near Guam, Mariana Forearc, Western Pacific	*Crenarchaeota*; Marine Group I & Marine Benthic Group B *Euryarchaeota*; *Methanobacteria* & *Methanosarcinales*/AMO (implicated)	Curtis et al., 2009 Mottl et al., 2003

‡ FeOB = iron-oxidizing bacteria. HSOB = hydrogen-oxidizing (anaerobic) or sulfur-oxidizing (aerobic) bacteria. SOB = sulfur-oxidizing bacteria. SRB = sulfur-reducing bacteria; AMO = anaerobic methane oxidation.
* First publication to detect both Epsilonproteobacteria (PVB OTU 2) and Zetaproteobacteria (PVB OTU 4) at a hydrothermal vent.

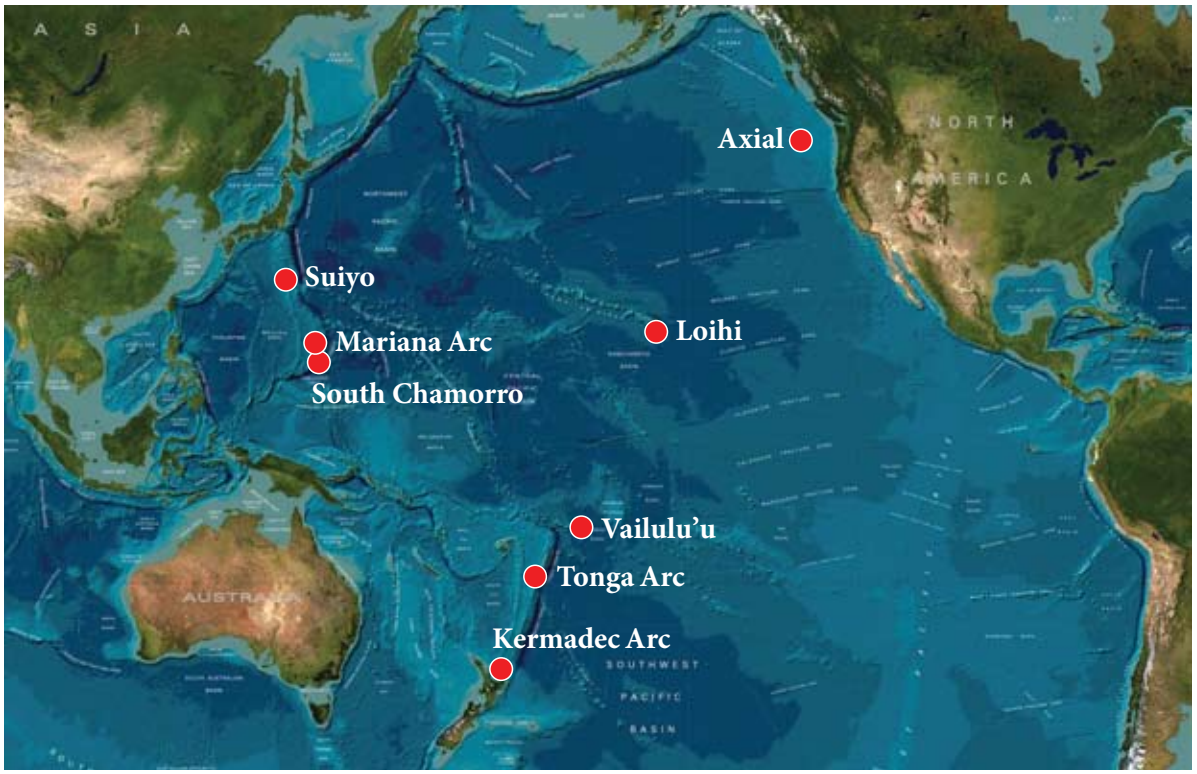

Figure 2. Pacific Ocean bathymetric map showing the locations where seamounts have been microbiologically investigated. These include (north to south): Axial Seamount, Suiyo Seamount, Lō`ihi Seamount, the Mariana Arc (n = 8), South Chamorro Seamount and Mariana Forearc (n = 7), Vailulu'u Seamount, the Tonga Arc (n = 2), and the Kermadec Arc (n=3). *Image reproduced with permission from the GEBCO world map (http://www.gebco.net/)*

at Lō`ihi, which used a cultivation-independent approach, was conducted prior to the 1996 eruption and showed that the class Epsilonproteobacteria (PVB OTU 2) dominated the surrounding microbial mats and that members of the newly discovered class Zetaproteobacteria (PVB OTU 4) were also present (Moyer et al., 1995). Phylum Proteobacteria is the largest, most diverse, and well-studied bacterial phylum, with representatives found in almost all habitats and metabolic conditions on Earth. It consists of five recognized classes, including Epsilonproteobacteria. As a result of subsequent studies at Lō`ihi, it was demonstrated that Zetaproteobacteria could represent a novel, sixth candidate class of Proteobacteria (Emerson and Moyer, 2002; Emerson et al., 2007). This conclusion was based on the isolation of a novel genus and species, *Mariprofundus ferrooxydans,* from an iron-rich mat at Lō`ihi. *M. ferrooxydans* is a chemoautotrophic, neutrophilic Fe-oxidizing bacterium that gains its energy for growth by oxidizing ferrous (Fe^{2+}) to ferric (Fe^{3+}) iron, and fixes CO_2. Furthermore, as it grows, it produces a stalklike structure composed primarily of Fe-oxyhydroxides, the waste product of the Fe-oxidation reaction that remains behind after the cells are gone (Emerson et al., 2007). These stalk-like structures are a common feature of many of the microbial mats at Lō`ihi, and are an easily identified diagnostic indicator that Fe-oxidizing bacteria are present (Figure 3).

More recently, it has been shown that Zetaproteobacteria dominate vent-site colonies in and around Lō`ihi, though colonization by Epsilonproteobacteria is also possible, most notably at higher-temperature (> 40°C) vents, demonstrating both spatial and temporal heterogeneity among these microbial mat communities (Rassa et al., 2009). An extensive analysis of multiple mat communities sampled from Lō`ihi using the DNA fingerprinting technique known as terminal restriction fragment length polymorphism

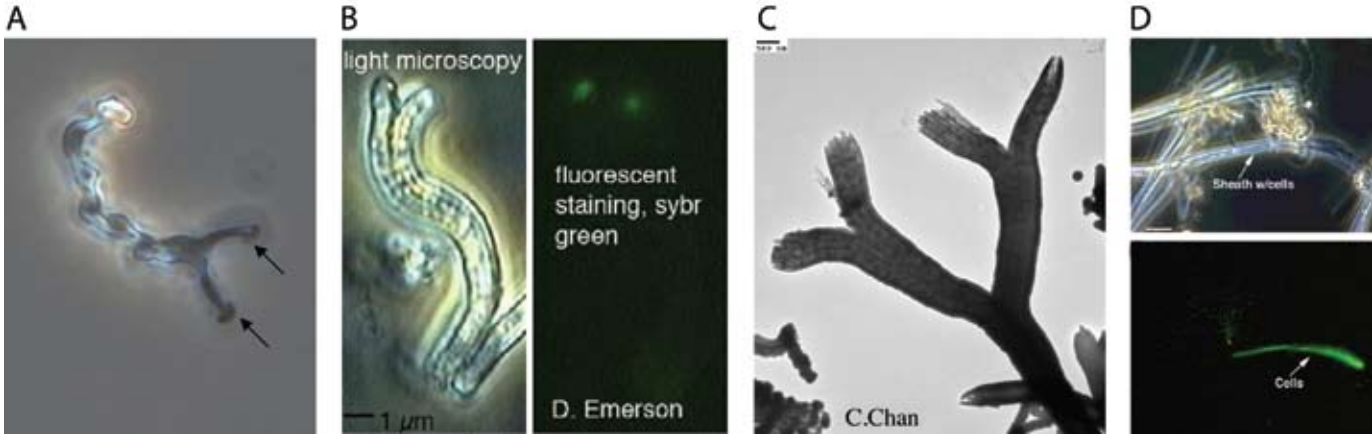

Figure 3. Morphotypes of Fe-oxidizing bacteria commonly observed at seamounts. (A) A light micrograph of *Mariprofundus ferrooxydans*, showing the twisted iron oxyhydroxide stalk with two cells, denoted by arrows, growing at the ends. (B) A light micrograph of an unknown organism that forms tubular iron oxide structures; the fluorescent dye image shows two cells present at the apical end of the structure, which is formed as the cells grow. (C) A transmission electron microscopy image of the same organism as shown in B; note that each time the cell divides the structure bifurcates. (D) A sheath-forming Fe-oxidizing bacterium; most of the sheaths are empty tubes of iron oxyhydroxides formed by filaments of cells that grow within them. *(D) is reproduced with permission (Emerson and Moyer, 2002)*

(T-RFLP) has revealed that there appear to be two distinct community types, Lō`ihi Groups 1 and 2; the iron-based Group 1 is essentially dominated by Zetaproteobacteria and the sulfur-based Group 2 by Epsilonproteobacteria (Figure 4). Their distributions seem to be linked to both geochemistry and temperature, with Group 1 common at lower-temperature vents (median temperature = 23°C) where there are fewer overall community members and Group 2 found at higher-temperature vents (median temperature = 77°C) exhibiting a higher diversity of detectable populations. We have correlated these results with the Group 1 communities associated with vents that have higher levels of dissolved Fe^{2+} and Group 2 communities with both high H_2S and Fe^{2+} concentrations (data not shown). We hypothesize that Group 1 communities are enhanced with members of Fe-oxidizing bacteria (Zetaproteobacteria), and that the Group 2 communities are enhanced with members of S-oxidizing bacteria (Epsilonproteobacteria) but still retain some of the Zetaproteobacteria.

Axial Seamount

Although Axial Seamount is located along the central portion of the Juan de Fuca Ridge (a mid-ocean ridge spreading center), it also lies at the eastern end of the Cobb-Eickelberg seamount chain. Axial originated at the Cobb hotspot, which generates lavas without a typical deep mantle chemical signature (see Spotlight 1 on page 38 of this issue [Chadwick et al., 2010]; Rhodes et al., 1990). This seamount was intensely studied after an eruptive event in 1998 (Embley et al., 1999), and members of the Epsilonproteobacteria were shown to dominate diffuse flow vents (Huber et al., 2003). Microbial samples from other diffuse-flow vent sites in the caldera analyzed by light microscopy, scanning electron microscopy (SEM), and X-ray diffraction (XRD) showed distinct morphologies, for example, iron-encrusted stalks similar to those of Zetaproteobacteria (Kennedy et al., 2003). Multiple microbial mat samples from across Axial's caldera have been examined using T-RFLP with the majority dominated by Epsilonproteobacteria and a few dominated by Zetaproteobacteria (data not shown). Surprisingly, this fits the pattern seen at Lō`ihi Seamount in terms of two distinct groups of bacterial-dominated community types (e.g., Figure 4); however, in this locatio the Epsilonproteobacteria were acting as the primary colonizers at a majority of vent sites shortly after an eruptive event that occurred in 1998 (Moyer an Engebretson, 2002).

Vailulu'u Seamount

Vailulu'u marks the current position of the Samoan hotspot in the southwester Pacific Ocean and exhibits active volcanism and hydrothermal venting that includes Fe-oxide rich floc, but also sulfidic vents (see Spotlight 8 on page

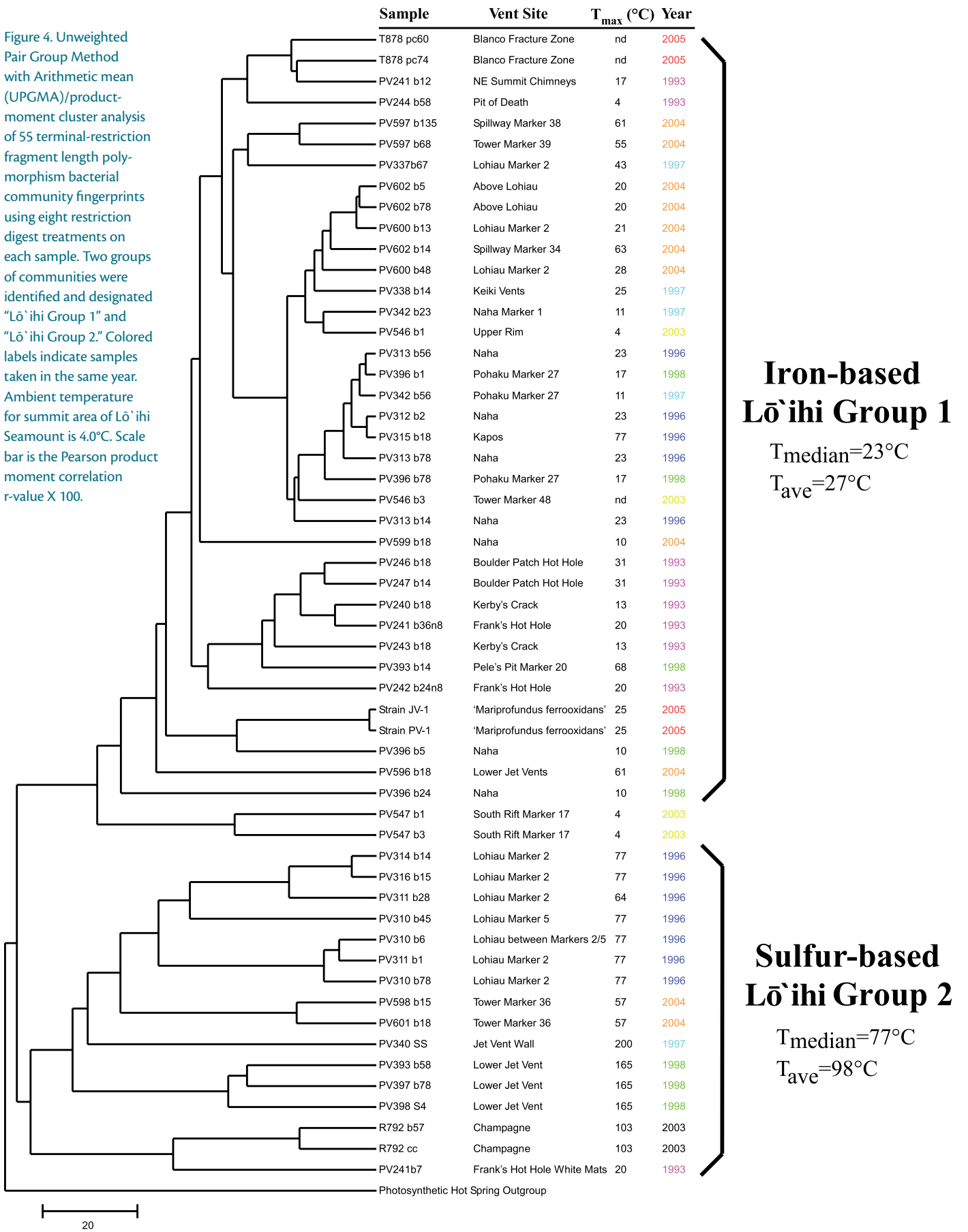

Figure 4. Unweighted Pair Group Method with Arithmetic mean (UPGMA)/product-moment cluster analysis of 55 terminal-restriction fragment length polymorphism bacterial community fingerprints using eight restriction digest treatments on each sample. Two groups of communities were identified and designated "Lō`ihi Group 1" and "Lō`ihi Group 2." Colored labels indicate samples taken in the same year. Ambient temperature for summit area of Lō`ihi Seamount is 4.0°C. Scale bar is the Pearson product moment correlation r-value X 100.

164 of this issue [Koppers et al., 2010]; Staudigel et al., 2006). Microbial samples from Vailulu'u have been analyzed using both cultivation-dependent and -independent approaches. Standard clone library analysis with small subunit ribosomal gene (SSU rDNA) biomarkers found that the majority of clones represented Epsilonproteobacteria, though Zetaproteobacteria were also detected (Sudek et al., 2009). In addition, a diverse fungal community, including several species of yeast, was found associated with iron mats as well as with basaltic rock surfaces at Vailulu'u (Connell et al., 2009). Unlike Lō`ihi, the complex circulation patterns created by Vailulu'u's summit crater provide habitat for a much more diverse and abundant macrofaunal community, including shrimp and eels. One result of these flow patterns is the existence of a "moat of death" where fish and other larger animals become entrapped in anoxic water and suffocate, providing a food source for anaerobic bacteria. The specific nutrient dynamics that support the macrofauna, including the role of bacterial primary production, have yet to be fully understood at Vailulu'u.

Suiyo Seamount

Suiyo Seamount is an active submarine volcano located on the volcanic front of the Izu-Bonin Arc, western Pacific Ocean, near Japan. It has a 200–300-m deep caldera at its summit with many active hydrothermal vents rich in hydrogen sulfide and methane that have recently been accessed through shallow drilling (Ishibashi et al., 2007). A number of novel thermophilic bacteria and archaea have been isolated from this seamount, including new chemoautotrophic species of bacteria that can use hydrogen as an energy source (Takai et al., 2003; Nakagawa et al., 2003), as well as an archaeon that can grow anaerobically with hydrogen and thiosulfate (Mori et al., 2008). Other microbial studies have included an examination of the hydrothermal plume within the caldera, which identified two dominant phylotypes of putative sulfur-oxidizing bacteria, the SUP01 group, belonging to Epsilonproteobacteria, and the SUP05 group, in the class Gammaproteobacteria (Sunamura et al., 2004). These phylotypes were distinct from those common in the surrounding seawater and accounted for up to 66% of the bacteria in the hydrothermal plume. This large percentage suggests that the hydrodynamics of the vent plume within the caldera create an incubator for these two groups of microbes. Another microbial study at Suiyo used a series of novel catheter-type in situ growth chambers inserted into subsurface boreholes after excavation with a portable submarine driller. In this case, a diverse array of phylotypes from Epsilonproteobacteria were found (Higashi et al., 2004). An extensive examination of borehole and vent fluids detected Gammaproteobacteria (including *Thiomicrospira* and *Alcanivorax*) in all samples, while multiple samples also exhibited Epsilonproteobacteria as well as a diverse array of potentially seawater-entrained bacterial phylotypes (Kato et al., 2009). Another study compared the diversity and distribution of integrase and integron genes (generally thought to be responsible for lateral gene transfer between unrelated bacterial groups) at Suiyo Seamount and at the Fryer site (aka Pika site) of the Mariana backarc (Elsaied et al., 2007). Many novel members of these gene families were discovered at both sites, suggestin that gene exchange between different bacteria at these sites could potentially be very common. Interestingly though, the results indicated that the two different vent communities harbored quite different sets of integron genes th were not necessarily compatible with one another. This observation suggests that lateral gene transfer may take place between populations within a vent site, but that gene transfer between geograp ically separated vent communities wou not happen as readily. This lack of later gene transfer is in contrast with antibiotic-resistant genes carrying integrons, where disparate environmental popula tions have been shown to have commo integron functions (Elsaied et al., 2007)

Mariana Arc Seamounts

The recent Ring of Fire expeditions to multiple seamounts in the Mariana Arc made several exciting discoveries that helped in the establishment of the new Marianas Trench Marine National Monument by the US government. During these expeditions, scientists observed, for the first time, a deep-sea eruption at Brimstone Pit on Northwes Rota-1, found pools of black-encrusted molten sulfur at Daikoku, witnessed the overlap between chemosynthetic filamentous microbial mats covering photosynthetic encrusting red algae an coral at Mat City near the summit of Ea Diamante (at a depth of only 200 m), a sampled white flocculent microbial ma next to white smoker chimneys venting liquid CO_2 droplets at Champagne Ven on Northwest Eifuku (see Spotlight 1 o page 38 of this issue [Chadwick et al.,

2010]; Embley et al., 2007). In a recent microbial study of 25 microbial communities from 18 different hydrothermal systems located at seven Mariana Arc volcanoes, a remarkable diversity of vent ecosystem environments was found, including black smokers (220°C), white smokers rich in CO_2, vents with high sulfide concentrations, as well as iron-rich vents (Davis and Moyer, 2008). Molecular fingerprinting analysis found that the community composition at each vent was unique, indicating a substantial degree of diversity in the microbial populations that inhabit these ecosystems; however, the majority of the communities examined were chemosynthetic and either dominated by Epsilonproteobacteria (Mariana Cluster III) or by Zetaproteobacteria (Mariana Cluster I) as determined by T-RFLP. Interestingly, even though conditions at these seamounts were sometimes extreme, bacteria were always dominant over archaea, with none of the communities containing more than 13% archaea (Davis and Moyer, 2008).

In a previous Mariana Arc study, dense microbial mats were observed covering white-smoker sulfur chimneys in TOTO caldera, of Paton-Masala Seamount, with temperatures up to 170°C. Samples collected from the chimney surface and interior, and from an in situ colonization system indicated that the microbial communities were dominated by Epsilonproteobacteria that were either hydrogen and/or sulfur oxidizers or anaerobic hydrogen-oxidizing, sulfur-reducing chemoautotrophs. This study also showed that these microbial communities contained no more than 2% archaea (Nakagawa et al., 2006). Combined, both of these microbial studies show a high degree of phylogenetic diversity as well as putative metabolic potential across the Epsilonproteobacteria. These data also fit the general pattern that either Epsilonproteobacteria or Zetaproteobacteria dominate the majority of seamount vent microbial communities. Figure 5 shows some characteristic microbial mat habitats dominated by either Zetaproteobacteria (Figure 5A and 5B) or those dominated by Epsilonproteobacteria (Figure 5C and 5D). Overall, the Mariana Arc and backarc support ecosystems that represent a bacterial biodiversity hotspot are thought to result from the complex geochemistry of these hydrothermal systems driven by the heterogeneity of the subducting source material coupled with the enhanced volcanic activity of the region (Davis and Moyer, 2008).

Tonga Arc Seamounts

Manned submersible dives along the Tonga Arc revealed two shallow-water volcanoes. Volcano 19 exhibited relatively high-temperature venting (245–265°C) in a depth range of 385–540 m and in some cases chimneys that had a distinctive "flamelike" discharge caused by an instantaneous phase separation upon the release of vent fluids. Volcano 1 exhibited more widespread diffuse venting (30–70°C), though both had extensive areas with filamentous microbial mats associated with Fe-oxyhydroxide mineral crusts (Stoffers et al., 2006). Samples from both locations were composed primarily of two-line ferrihydrite, and transmission electron microscopy (TEM) revealed structures similar to those formed by *M. ferrooxydans*, supporting the assumption that these are biogenic iron oxides (Langley et al., 2009). Molecular microbial analysis of similar samples from both Volcanoes 1 and 19 detected the presence of multiple Zetaproteobacteria phylotypes, representing a high degree of diversity within this group. In addition, these Fe-oxidizing bacteria were most abundant at Volcano 1, where sediments were richer in Fe and contained more crystalline forms of Fe oxides (Forget et al., in press).

Kermadec Arc Seamounts

The Kermadec-Tonga Arcs, together the longest submarine arc system on the planet, contain a series of recently explored seamounts (deRonde et al., 2001, 2007). Microbial samples have been collected at Brothers Volcano, from the caldera vent field, and at the lower cone site. At the caldera vent field, the exteriors of high-temperature (up to 290°C) black smoker chimneys were dominated by variable communities of bacteria, including a majority of putative sulfur-oxidizing Epsilonproteobacteria and Gammaproteobacteria (Takai et al., 2009). A single piece of dacite lava covered with elemental sulfur and white microbial mats was collected at the lower cone site from 67°C vent effluent and analyzed using standard molecular microbial techniques. In this study, the most abundant phylotypes detected were from the class Deltaproteobacteria (most closely related to sulfate-reducing bacteria). However, 5% of this clone library was represented by Epsilonproteobacteria phylotypes (Stott et al., 2008). Another recent microbial study from two more seamounts (Clark and Tangaroa) on the southern

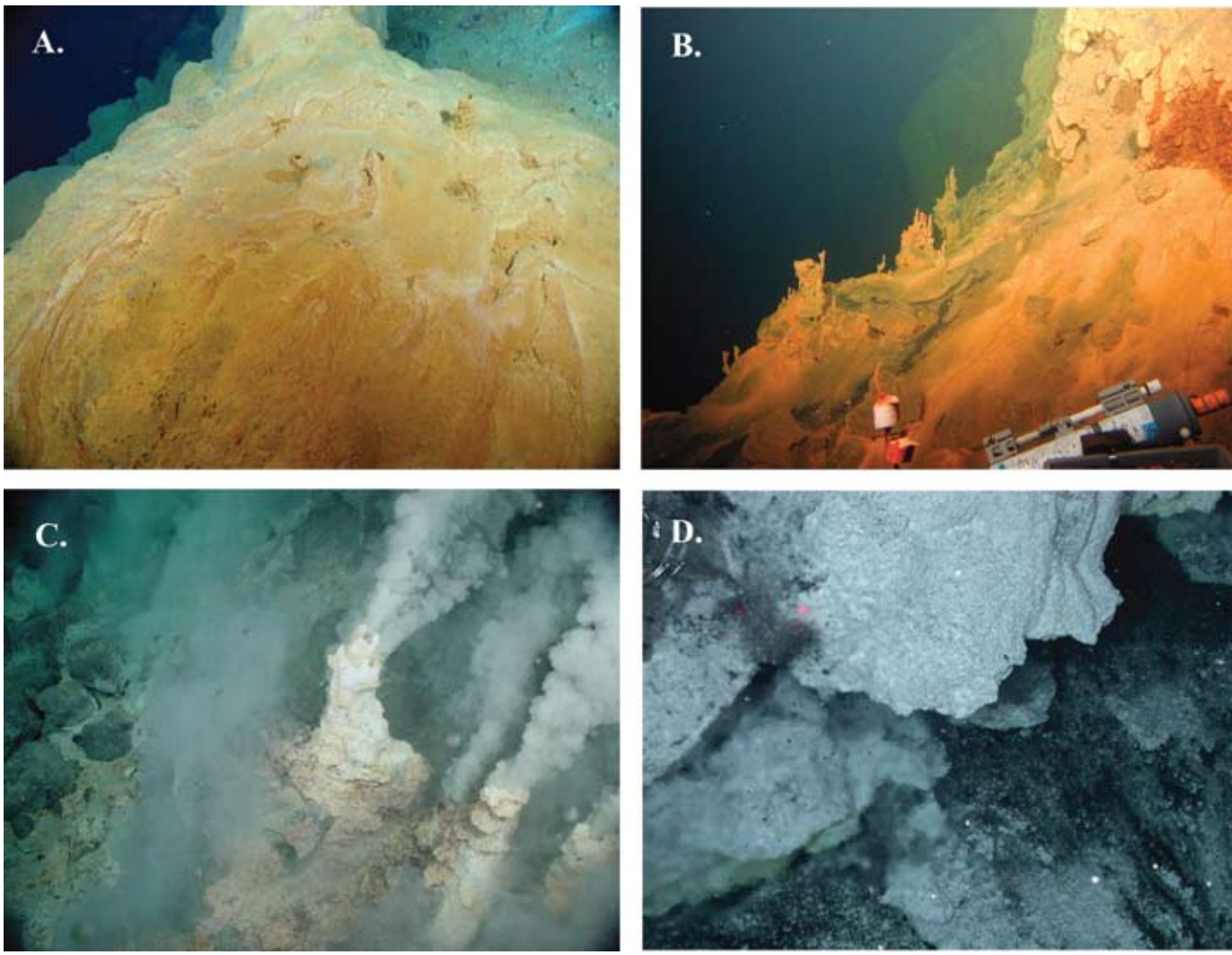

Figure 5. Photographs of microbial mats collected by remotely operated vehicle. (A) Iron-oxide-encrusted microbial mat at Yellow Top Vent, Northwest Eifuku (B) Small chimneys and iron oxide microbial mats inside Pele's Pit Crater at Upper Hiolo Vents, Lō`ihi. (C) White smoker vents covered with microbial mats at Champagne Vents, Northwest Eifuku. (D) White microbial mats covering rocks at Iceberg Vent, Northwest Rota-1.

Kermadec Arc, revealed extensive zones of flocculent iron oxides on the order of tens to hundreds of square meters. Morphologically, these microbial mats resembled the biogenic oxides found at Lō`ihi and elsewhere. Phylotypes of the Zetaproteobacteria were detected in each of the three mats examined; however, the clone libraries were dominated (67% of the total number of clones) by members of the Epsilonproteobacteria. T-RFLP fingerprinting analysis of five Fe-floc and two sediment samples showed that a majority of these samples contained detectable Zetaproteobacteria peaks. These findings from the southern Kermadec Arc suggest that we may not fully understand the story of iron-oxidizing bacterial communities associated with seamounts. Either there may be a group of as-of-yet uncultured Fe-oxidizers that are Epsilonproteobacteria (facilitating the formation of Fe-floc microbial mats), or perhaps the Fe-oxidizing Zetaproteobacteria are only active in rapidly accreting mats (Hodges and Olsen, 2009).

South Chamorro and Other Mariana Forearc Seamounts

The Mariana forearc is comprised of a series of serpentine mud volcanoes formed between the Mariana Trench and the volcanic arc that lies to its west (Fryer et al., 1999). Dehydration

reactions within the subducting plate transform the overriding plate into a hydrated composite of serpentinite, mud, and fluids that extrudes from fault-derived conduits, resulting in giant mud volcanoes. These mud volcanoes reach sizes up to 50 km in diameter and 2 km in height (Fryer et al., 2006). In addition, springs often form (as a byproduct of the upwelling fluid, attributed to the sediment compaction and dehydration process) and deliver water to the seafloor that is typically fresher than seawater and highly alkaline, with pH up to 12.5 (see Spotlight 9 on page 174 of this issue [Wheat et al., 2010]; Mottl et al., 2003, 2004).

South Chamorro Seamount has active summit springs (Figure 6). This area was the focus of an Ocean Drilling Program (ODP) investigation (Leg 195, Site 1200) into the structure and diversity of the microbial populations existing near the seamount surface and at depth below the seafloor. In general, these highly alkaline fluids also contain elevated levels of dissolved sulfide with nearly no sulfate, which is attributed to both anaerobic methane oxidation (AMO) and sulfate reduction in a microbial habitat overwhelmingly dominated by archaea (Mottl et al., 2003). Mariana forearc mud volcanoes thus provide a unique biogeochemical view into the process of devolatization of a subducting slab and the serpentinization processes within the overriding plate as mechanisms for fueling subsurface communities of extremophilic archaea. This habitat also

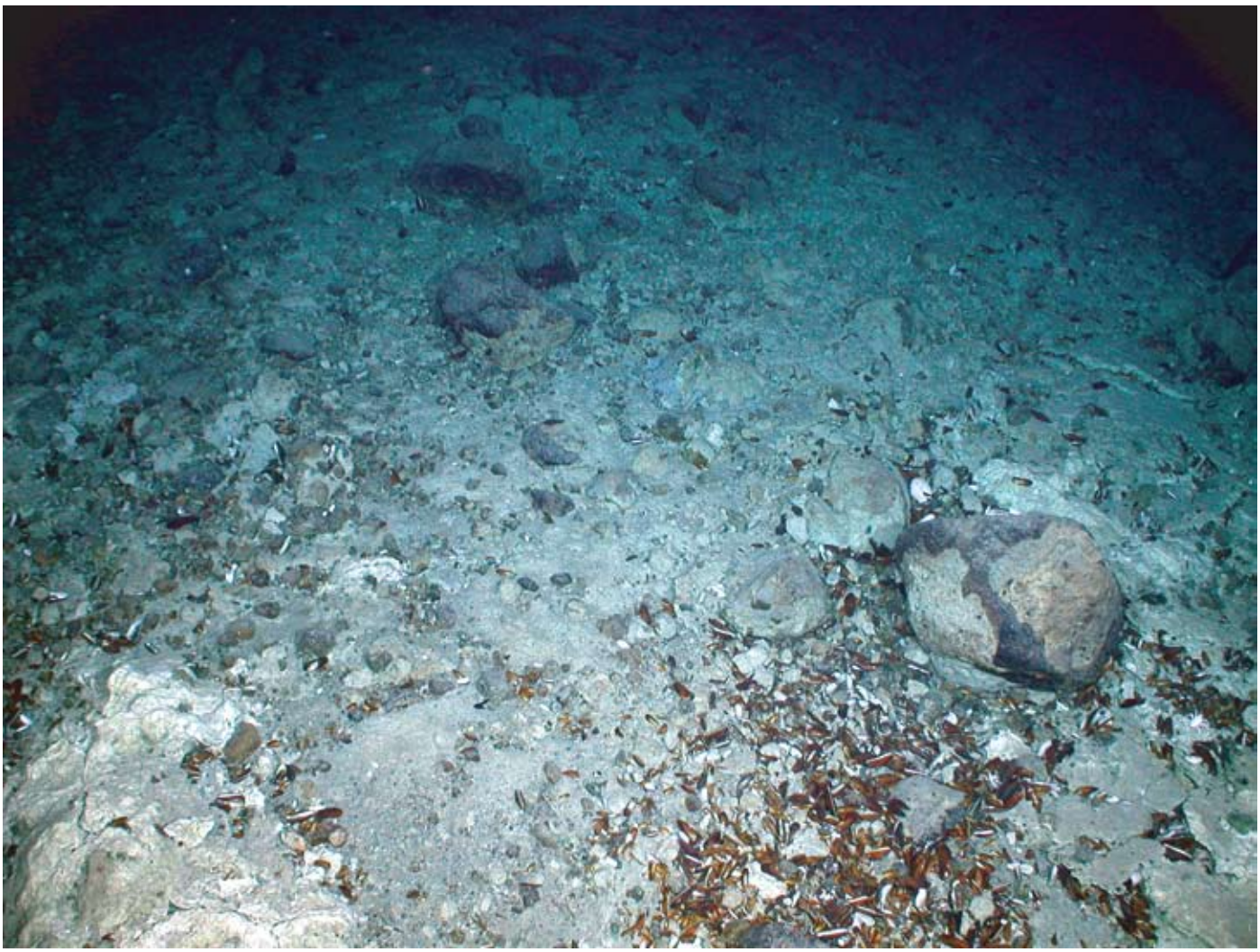

Figure 6. Summit springs at South Chamorro Seamount showing bathymodiolid mussels present. Photo taken from submersible *Shinkai 6500* view port. *Courtesy of Patty Fryer, University of Hawai`i*

provides an excellent opportunity for microbial investigation of phylogenetic diversity and ecological significance in an extreme subsurface environment representing the upper pH limit for life (Takai et al., 2005).

A recent molecular microbial study revealed new populations of archaea that exist at the seafloor in serpentinized muds from South Chamorro Seamount. Archaeal communities from seven Mariana forearc seamounts were assessed with T-RFLP, while two sites atop South Chamorro were also investigated using clone library analysis. Though a bacterium (*Marinobacter alkaliphilus*) was previously isolated from ODP Site 1200 seafloor muds (Takai et al., 2005), no bacteria were detected using PCR-based molecular methods. Novel *Crenarcheaota* phylotypes, from within Marine Group I and Marine Benthic Group B, as well as *Euryarcheaota* phylotypes from the *Methanobacteria* and *Methanosarcinales*, were detected. T-RFLP fingerprinting revealed that similar archaeal communities from Big Blue and Blue Moon seamounts were nearly identical to the South Chamorro ODP Hole 1200E site, which was hypothesized to correlate with active summit spring habitats (Curtis et al., 2009).

EMERGING PATTERNS REGARDING COMMUNITY STRUCTURE

There is growing evidence, as summarized in Table 1, that Zetaproteobacteria and/or Epsilonproteobacteria are the most common members of surface hydrothermal habitats associated with volcanically active seamounts. Somewhat surprisingly, archaea tend not to be abundant in the surface habitats sampled at seamounts, although they are far more abundant in the interior of high-temperature chimneys and anaerobic subsurface fluids at volcanically active seamounts (Huber et al., 2002; Takai et al., 2009). A notable exception are the mud volcanoes from Mariana forearc, which represent some of the most extremely alkaline habitats on Earth and appear to be dominated by unusual archaea (Curtis et al., 2009). Overall, microbial community patterns must reflect the underlying geochemistry that is driven by seamount geologic processes; for example, neither Epsilonproteobacteria or Zetaproteobacteria are common members of the seawater surrounding seamounts.

> “...SEAMOUNTS POTENTIALLY REPRESENT HOTSPOTS OF MICROBIAL DIVERSITY, YET OUR UNDERSTANDING OF THE MICROBIOLOGY OF SEAMOUNTS IS STILL IN ITS INFANCY.”

As mentioned earlier, the Epsilonproteobacteria are comprised of a large breadth and depth of phylogenetic diversity. Significant effort has gone into cultivating representatives for each of the various groups that have been described using cultivation-independent approaches based on the analysis of SSU rDNA clone libraries. A recent review finds that all cultures characterized as hydrothermal-vent-associated Epsilonproteobacteria either oxidize reduced sulfur or reduce sulfur while oxidizing hydrogen or formate. Although most are autotrophs, they can also be mixotrophs and occasionally heterotrophs (Campbell et al., 2006). For example, the phylotypes most often found at Lō`ihi are from within the *Sulfurovum* and *Sulfurimonas* groups (sulfur oxidizers), although *Nitratiruptor* group (hydrogen-oxidizing, sulfur-reducer) phylotypes have also been detected (Moyer et al., 1995; Rassa et al., 2009; Figure 7).

The emerging discovery of Zetaproteobacteria associated with diffuse vents that are rich in available Fe^{2+} is intriguing. On the basis of morphology, it has been recognized since the 1980s that conspicuous iron-oxide-encrusted stalks, presumed to be of biogenic origin, were commonly found in flocculent iron oxyhydroxide deposits collected from modern and ancient hydrothermal sites (Juniper and Fouquet 1988). It was the isolation of *M. ferrooxydans* and analysis of its SSU rDNA (as well as other evolutionary conserved genes) that suggested it represented a novel class of Proteobacteria (Emerson et al., 2007). While this group of microbes was initially thought to be very rare, follow-up studies are suggesting that Zetaproteobacteria can be quite abundant at seamount habitats rich in iron. The fact that *M. ferrooxydans* is in cultu

does not mean that we have described all the important Zetaproteobacteria. Indeed, it appears that *M. ferrooxydans* may represent a lineage that is relatively minor at most sites (Figure 3A). Morphological information from the mats at Lō`ihi also provide tantalizing evidence that other "morphotypes" of Fe-oxidizers exist. One common morphotype is an unusual flattened tubular iron-oxide structure with a single cell growing at the apical end. When the organism divides, the tube bifurcates into a characteristic Y shape, illustrated in Figure 3B and 3C. These structures are common in several of the mats at Lō`ihi, and in some cases outnumber other morphotypes of Fe-oxidizers.

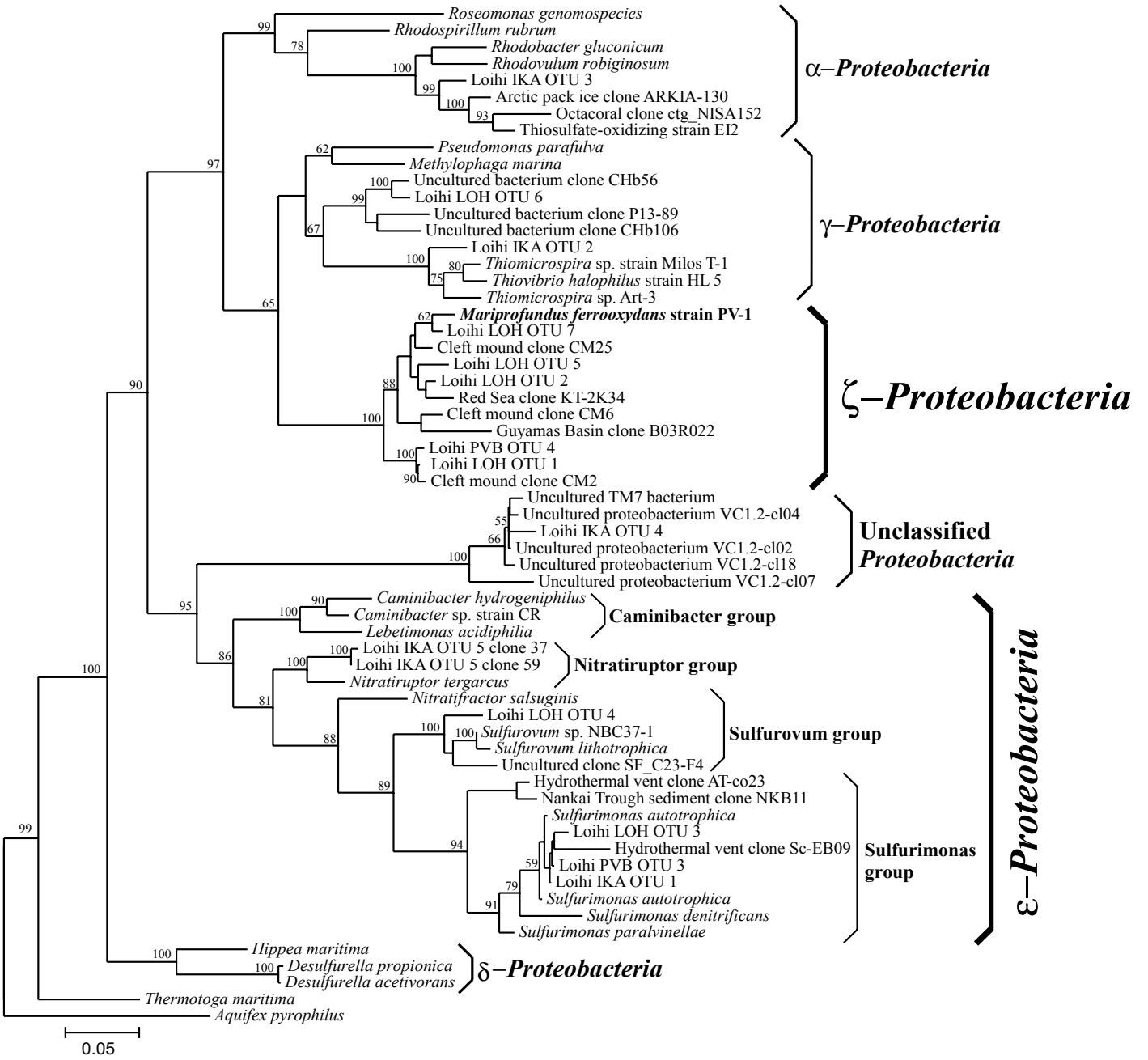

Figure 7. Maximum-likelihood phylogenetic tree showing the evolutionary placement of phylotypes belonging to Proteobacteria with emphasis on Zetaproteobacteria and Epsilonproteobacteria. Only bootstrap values above 50 are shown. Scale bar represents five nucleotide substitutions per 100 positions.

Another morphotype that is observed in certain Fe-rich microbial mats is a sheathed organism, illustrated in Figure 3D. Although this organism looks very much like the common freshwater Fe-oxidizer *Leptothrix ochracea*, we have not identified any phylotypes related to members of the class Betaproteobacteria, to which *Leptothrix* belongs. It is possible that these marine sheathed Fe-oxidizers represent a case of convergent evolution, where organisms that are quite different phylogenetically have found a common strategy to grow with iron. It is also quite possible, perhaps even likely, that not all Zetaproteobacteria are Fe-oxidizers, but that some might use other substrates for growth.

OPPORTUNITIES FOR MICROBIAL RESEARCH AT SEAMOUNTS ABOUND

In general, our understanding of the forces that shape microbial community structure within a given environment are in a state of flux, be it the human gut, salt marsh sediment, or the ocean's water column. The same can be said even more emphatically of seamounts, because they are poorly studied compared to these other environments. Nonetheless, seamounts have the potential to make good natural laboratories for studying basic problems having to do with microbial ecology and evolution. Because they tend to be geographically isolated from one another, there may be more of a barrier for movement of microorganisms between seamounts than is the case in the more contiguous environments of a mid-ocean ridge. Thus, seamounts could represent repositories for studying the biogeography of microbial populations. In addition, many other basic questions remain:

- Are there fundamental differences in microbial communities at seamounts where hydrothermal processes prevail compared to mid-ocean ridges? Is iron-oxidation a more important process at seamounts than at ridge-axis spreading centers?
- Are seamounts windows into a subsurface world? How important are subseafloor circulation paths for the redistribution of microbes? Can microbes themselves influence these patterns by altering the subsurface flow regimes?
- To what extent do water-column hydrodynamics associated with seamounts influence microbial community structure and dynamics through their influence on ocean dynamics and changes in nutrient distribution patterns?
- How important are seamounts to global marine geomicrobiology and what is their role in altering the crust and ocean chemistry, including iron and sulfur cycling in the ocean? How might seamounts affect ocean acidification and the global carbon cycle?

These types of questions illustrate both how limited our understanding is of undersea microbial ecosystems, and also how much potential remains for significant new discoveries in marine microbiology. In addition to contributing new knowledge about fundamental processes at the ocean floor and in the subsurface, it is possible that novel compounds, enzymes, or organisms could be discovered from seamounts that would have practical applications in the biotechnology, bioenergy, or bioremediation sectors. It is even possible that microbes from seamounts could provide important clues about the origin of life on Earth and its potential to exist in other habitable zones in the solar syste

ACKNOWLEDGMENTS

We thank Clara Chan for use of the TEM image used in Figure 3C. This work was supported in part by grants from the National Science Foundation (MCB-0348330 to DE; MCB-0348734 and OCE-0727086 to CLM) and by funding from the NASA Astrobiology Institute (to DE).

REFERENCES

Campbell, B.J., A.S. Engel, M.L. Porter, and K. Takai. 2006. The versatile ε-proteobacteria: Key players in sulphidic habitats. *Nature Reviews Microbiology* 4:458–468.

Chadwick, W.W., D.A. Butterfield, R.W. Embley, V. Tunnicliffe, J.A. Huber, S.L. Nooner, and D.A. Clague. 2010. Spotlight 1: Axial Seamou *Oceanography* 23(1):38–39

Chivian, D., E.L. Brodie, E.J. Alm, D.E. Culley, P.S. Dehal, T.Z. DeSantis, T.M. Gihring, A. Lapidus, L.-H. Lin, S.R. Lowry, and others. 2008. Environmental genomics reveals a single-species ecosystem deep within Earth. *Science* 322:275–278.

Connell, L., A. Barrett, A. Templeton, and H. Staudigel. 2009. Fungal diversity associated with an active deep sea volcano: Vailulu'u Seamount, Samoa. *Journal of Geomicrobiology* 26:597–605.

Cowen, J.P., S.J. Giovannoni, F. Kenig, H.P. Johnson, D. Butterfield, M.S. Rappe, M. Hutnak, and P. Lam. 2003. Fluids from aging ocean crust that support microbial life. *Science* 299:120–123.

Curtis, A.C., C.G. Wheat, P. Fryer, and C.L. Moye 2009. Mariana forearc serpentine mud volcanoes harbor novel communities of extre mophilic *Archaea*. Poster Abstracts: IODP New Ventures in Exploring Scientific Targets (INVEST), September 23–25, 2009, Bremen, Germany.

Davis, R.E., and C.L. Moyer. 2008. Extreme spati and temporal variability of hydrothermal microbial mat communities along the Marian Island Arc and southern Mariana back-arc system. *Journal of Geophysical Research* 113, B08S15, doi:10.1029/2007JB005413.

deRonde, C.E.J., E.T. Baker, G.J. Massoth, J.E. Lupton, I.C. Wright, R.A. Feely, and R.R. Greene. 2001. Intra-oceanic subduction-

related hydrothermal venting, Kermadec volcanic arc, New Zealand. *Earth and Planetary Science Letters* 193:359–369.

deRonde, C.E.J., E.T. Baker, G.J. Massoth, J.E. Lupton, I.C. Wright, R.J. Sparks, S.C. Bannister, M.E. Reyners, S.L. Walker, R.R. Greene, and others. 2007. Submarine hydrothermal activity along the mid-Kermadec Arc, New Zealand: Large-scale effects on venting. *Geochemistry, Geophysics, Geosystems* 8(7), Q07007, doi:10.1029/2006GC001495.

Duennebier, F.K., N.C. Becker, J. Caplan-Auerbach, D.A. Clague, J. Cowen, M. Cremer, M. Garcia, F. Goff, A. Malahoff, G.M. McMurtry, and others. 1997. Researchers rapidly respond to submarine activity at Loihi Volcano, Hawaii. *Eos, Transactions, American Geophysical Union* 78:229–233.

Edwards, K.J., W. Bach, and T.M. McCollom. 2005. Geomicrobiology in oceanography: Microbe-mineral interactions at and below the seafloor. *TRENDS in Microbiology* 13:449–456.

Elsaied, H., H.W. Stokes, T. Nakamura, K. Kitamura, H. Fuse, and A. Maruyama. 2007. Novel and diverse integron integrase genes and integron-like gene cassettes are prevalent in deep-sea hydrothermal vents. *Environmental Microbiology* 9:2,298–2,312.

Embley, R.W., E.T. Baker, D.A. Butterfield, W.W. Chadwick, J.E. Lupton, J.A. Resing, C.E.J. de Ronde, K. Nakamura, V. Tunnicliffe, J. Dower, and S.G. Merle. 2007. Exploring the submarine ring of fire, Mariana Arc–Western Pacific. *Oceanography* 20(4):68–79.

Embley, R.W., W.W. Chadwick, D. Clague, and D. Stakes. 1999. 1998 Eruption of Axial Volcano: Multibeam anomalies and seafloor observations. *Geophysical Research Letters* 26:3,425–3,428.

Emerson, D., and C.L. Moyer. 2002. Neutrophilic Fe-oxidizing bacteria are abundant at the Loihi Seamount hydrothermal vents and play a major role in Fe oxide deposition. *Applied and Environmental Microbiology* 68:3,085–3,093.

Emerson, D., J.A. Rentz, T.G. Lilburn, R.E. Davis, H. Aldrich, C. Chan, and C.L. Moyer. 2007. A novel lineage of Proteobacteria involved in formation of marine Fe-oxidizing microbial mat communities. *PLoS ONE* 2:e667, doi:10.1371/journal.pone.0000667.

Fisher, A.T., and C.G. Wheat. 2010. Seamounts as conduits for massive fluid, heat, and solute fluxes on ridge flanks. *Oceanography* 23(1):74–87.

Forget, N.L., S.A. Murdock, and S.K. Juniper. In press. Bacterial diversity in Fe-rich hydrothermal sediments at two South Tonga Arc submarine volcanoes. *Geobiology*.

Fryer P., J. Gharib, K. Ross, I. Savov, and M.J. Mottl. 2006. Variability in serpentinite mudflow mechanisms and sources: ODP drilling results on Mariana forearc seamounts. *Geochemistry, Geophysics, Geosystems* 7(8), Q08014, doi:10.1029/2005GC001201.

Fryer, P., C.G. Wheat, and M.J. Mottl. 1999. Mariana blueschist mud volcanism: Implications for conditions within the subduction zone. *Geology* 27:103–106.

Glazer, B.T., and O.J. Rouxel. 2009. Redox speciation and distribution within diverse iron-dominated microbial habitats at Loihi Seamount. *Journal of Geomicrobiology* 26:606–622.

Gold, T. 1992. The deep, hot biosphere. *Proceedings of the National Academy of Sciences of the United States of America* 89:6,045–6,049.

Higashi, Y., M. Sunamura, K. Kitamura, K. Nakamura, Y. Kurusu, J. Ishibashi, T. Urabe, and A. Maruyama. 2004. Microbial diversity in hydrothermal surface to subsurface environments of Suiyo Seamount, Izu-Bonin Arc, using a catheter-type in situ growth chamber. *FEMS Microbiology Ecology* 47:327–336.

Hodges, T.W., and J.B. Olsen. 2009. Molecular comparison of bacterial communities within iron-containing flocculent mats associated with submarine volcanoes along the Kermadec Arc. *Applied and Environmental Microbiology* 75:1,650–1,657.

Huber, J.A., D.A. Butterfield, and J.A. Baross. 2002. Temporal changes in archaeal diversity and chemistry in a mid-ocean ridge subseafloor habitat. *Applied and Environmental Microbiology* 68:1,585–1,594.

Huber, J.A., D.A. Butterfield, and J.A. Baross. 2003. Bacterial diversity in a subseafloor habitat following a deep-sea volcanic eruption. *FEMS Microbiology Ecology* 43:393–409.

Huber, J.A., H.P. Johnson, D.A. Butterfield, and J.A. Baross. 2006. Microbial life in ridge flank crustal fluids. *Environmental Microbiology* 8:88–99.

Ishibashi, J., K. Marumo, A. Maruyama, and T. Urabe. 2007. Direct access to the sub-vent biosphere by shallow drilling. *Oceanography* 20(1):24–25.

Jørgensen, B.B., and A. Boetius. 2007. Feast and famine: Microbial life in the deep-sea bed. *Nature Reviews Microbiology* 5:770–781.

Juniper, S.K., and Y. Fouquet. 1988. Filamentous iron-silica deposits from modern and ancient hydrothermal sites. *Canadian Mineralogist* 26:859–869.

Karl, D.M. 1995. Ecology of free-living, hydrothermal vent microbial communities. Pp. 35–124 in *Microbiology of Deep-Sea Hydrothermal Vents*. D.M. Karl, ed., CRC Press, Boca Raton, FL.

Karl, D.M., G.M. McMurtry, A. Malahoff, and M.O. Garcia. 1988. Loihi Seamount, Hawaii: A mid-plate volcano with a distinctive hydrothermal system. *Nature* 335:532–535.

Kato, S., K. Hara, H. Kasai, T. Teramura, M. Sunamura, J. Ishibashi, T. Kakegawa, T. Yamanaka, H. Kimura, K. Marumo, T. Urabe, and A. Yamagishi. 2009. Spatial distribution, diversity and composition of bacterial communities in sub-seafloor fluids at a deep-sea hydrothermal field of the Suiyo Seamount. *Deep-Sea Research Part I* 56:1,844–1,855.

Kennedy, C.B., S.D. Scott, and F.G. Ferris. 2003. Ultrastructure and potential sub-seafloor evidence of bacteriogenic iron oxides from Axial Volcano, Juan de Fuca Ridge, northeast Pacific Ocean. *FEMS Microbiology Ecology* 43:247–254.

Koppers, A.A.P., H. Staudigel, S.R. Hart, C. Young, and J.G. Konter. 2010. Spotlight 8: Vailulu'u Seamount. *Oceanography* 23(1):164–165.

Langley, S., P. Igric, Y. Takahashi, Y. Sakai, D. Fortin, M.D. Hannington, and U. Schwarz-Schampera. 2009. Preliminary characterization and biological reduction of putative biogenic iron oxides (BIOS) from the Tonga-Kermadec Arc, Southwest Pacific Ocean. *Geobiology* 7:35–49.

Lavelle, J.W., and C. Mohn. 2010. Motion, commotion, and biophysical connections at deep ocean seamounts. *Oceanography* 23(1):90–103.

Mori, K., A. Maruyama, T. Urabe, K. Suzuki, and S. Hanada. 2008. *Archaeoglobus infectus* sp. nov., a novel thermophilic, chemolithoheterotrophic archaeon isolated from a deep-sea rock collected at Suiyo Seamount, Izu-Bonin Arc, western Pacific Ocean. *International Journal of Systematic and Evolutionary Microbiology* 58:810–816.

Mottl, M.J., S.C. Komor, P. Fryer, and C.L. Moyer. 2003. Deep-slab fluids fuel extremophilic *Archaea* on a Mariana forearc serpentinite mud volcano: Ocean Drilling Program Leg 195. *Geochemistry, Geophysics, Geosystems* 4(11), 9009, doi:10.1029/2003GC000588.

Mottl, M.J., C.G. Wheat, P. Fryer, J. Gharib, and J.B. Martin. 2004. Chemistry of springs across the Mariana forearc shows progressive devolatilization of the subducting plate. *Geochimica et Cosmochimica Acta* 68:4,915–4,933.

Moyer, C.L., and J.J. Engebretson. 2002. Colonization by pioneer populations of epsilon-Proteobacteria and community succession at mid-ocean ridge hydrothermal vents as determined by T-RFLP analysis. *Eos, Transactions, American Geophysical Union, Fall Meeting Supplement,* 83, Abstract V11C-12.

Moyer, C.L., F.C. Dobbs, and D.M. Karl. 1995. Phylogenetic diversity of the bacterial community from a microbial mat at an active, hydrothermal vent system, Loihi Seamount, Hawaii. *Applied and Environmental Microbiology* 61:1,555–1,562.

Nakagawa, S., and K. Takai. 2008. Deep-sea vent chemoautotrophs: Diversity, biochemistry and ecological significance. *FEMS Microbiology Ecology* 65:1–14.

Nakagawa, S., K. Takai, K. Horikoshi, and Y. Sako. 2003. *Persephonella hydrogeniphila* sp. nov., a novel thermophilic, hydrogen-oxidizing bacterium from a deep-sea hydrothermal vent chimney. *International Journal of Systematic and Evolutionary Microbiology* 53:863–869.

Nakagawa, T., K. Takai, Y. Suzuki, H. Hirayama, U. Konno, U. Tsunogai, and K. Horikoshi. 2006. Geomicrobiological exploration and characterization of a novel deep-sea hydrothermal system at the TOTO caldera in the Mariana Volcanic Arc. *Environmental Microbiology* 8:37–49.

Parkes, R.J., B.A. Cragg, and P. Wellsbury. 2000. Recent studies on bacterial populations and processes in subseafloor sediments: A review. *Hydrogeology Journal* 8:11–28.

Rassa, A.C., S.M. McAllister, S.A. Safran, and C.L. Moyer. 2009. Zeta-Proteobacteria dominate the colonization and formation of microbial mats in low-temperature hydrothermal vents at Loihi Seamount, Hawaii. *Geomicrobiology Journal* 26:623–638.

Rhodes, J.M., C. Morgan, and R.A. Liias. 1990. Geochemistry of Axial Seamount lavas: Magmatic relationship between the Cobb Hotspot and the Juan de Fuca Ridge. *Journal of Geophysical Research* 95:12,713–12,733.

Staudigel, H., and D.A. Clague. 2010. The geological history of deep-sea volcanoes: Biosphere, hydrosphere, and lithosphere interactions. *Oceanography* 23(1):58–71.

Staudigel, H., H. Furnes, N. McLoughlin, N.R. Banerjee, L.B. Connell, and A. Templeton. 2008. 3.5 billion years of glass bioalteration: Volcanic rocks as a basis for microbial life? *Earth-Science Reviews* 89:156–176.

Staudigel, H., S.R. Hart, A. Pile, B.E. Bailey, E.T. Baker, S. Brooke, D.P. Connelly, L. Haucke, C.R. German, I. Hudson, and others. 2006. Vailulu'u Seamount, Samoa: Life and death on an active submarine volcano. *Proceedings of the National Academy of Sciences of the United States of America* 103:6,448–6,453.

Staudigel, H., C.L. Moyer, M.O. Garcia, A. Malahoff, D.A. Clague, and A.A.P. Koppers. 2010. Spotlight 3: Lō`ihi Seamount. *Oceanography* 23(1):72–73.

Stoffers, P., T.J. Worthington, U. Schwarz-Schampera, M.D. Hannington, G.J. Massoth, R. Hekinian, M. Schmidt, L.J. Lundsten, L.J. Evans, R. Vaiomo'unga, and T. Kerby. 2006. Submarine volcanoes and high-temperature hydrothermal venting on the Tonga arc, Southwest Pacific. *Geology* 34:453–456.

Stott, M.B., J.A. Saito, M.A. Crowe, P.F. Dunfield, S. Hou, E. Nakasone, C.J. Daughney, A.V. Smirnova, B.W. Mountain, K. Takai, and M. Alam. 2008. Culture-independent characterization of a novel microbial community at a hydrothermal vent at Brothers Volcano, Kermadec arc, New Zealand. *Journal of Geophysical Research* 113, B08S06, doi:10.1029/2007JB005477.

Sudek, L.A., A.S. Templeton, B.M. Tebo, and H. Staudigel. 2009. Microbial ecology of Fe (hydr)oxide mats and basaltic rock from Vailulu'u Seamount, American Samoa. *Geomicrobiology Journal* 26:581–596.

Sunamura, M., Y. Higashi, C. Miyako, J. Ishibashi, and A. Maruyama. 2004. Two *Bacteria* phylotypes are predominant in the Suiyo Seamount hydrothermal plume. *Applied and Environmental Microbiology* 70:1,190–1,198.

Takai, K., C.L. Moyer, M. Miyazaki, Y. Nogi, H. Hirayama, K.H. Nealson, and K. Horikoshi. 2005. *Marinobacter alkaliphilus* sp. nov., a novel alkaliphilic bacterium isolated from subseafloor alkaline serpentine mud from Ocean Drilling Program Site 1200 at South Chamorro Seamount, Mariana Forearc. *Extremophiles* 9:17–27.

Takai, K., S. Nakagawa, A.-L. Reysenbach, J. Hoek. 2006. Microbial ecology of mid-ocean ridges and back-arc basins. Pp. 185–213 in *Back-Arc Spreading Systems: Geological, Biological, Chemical, and Physical Interactions*. D.M. Christie, C.R. Fisher, S.M. Lee, and S. Givens, eds, Geophysical Monograph Series 166, American Geophysical Union, Washington, DC.

Takai, K., S. Nakagawa, Y. Sako, and K. Horikoshi. 2003. *Balnearium lithotrophicum* gen. nov., sp. nov., a novel thermophilic, strictly anaerobic, hydrogen-oxidizing chemolithoautotroph isolated from a black smoker chimney in the Suiyo Seamount hydrothermal system. *International Journal of Systematic and Evolutionary Microbiology* 53:1,947–1,954.

Takai, K., K. Nakamura, T. Toki, U. Tsunogai, M. Miyazaki, J. Miyazaki, H. Hirayama, S. Nakagawa, T. Nunoura, and K. Horokoshi. 2008. Cell proliferation at 122°C and isotopically heavy CH_4 production by hyperthermophilic methanogen under high-pressure cultivation. *Proceedings of the National Academy of Sciences of the United States of America* 105:10,949–10,954.

Takai, K., T. Nunoura, K. Horikoshi, T. Shibuya, K. Nakamura, Y. Suzuki, M. Stott, G.J. Massoth, B.W. Christenson, C.E.J. deRonde, and others. 2009. Variability in microbial communities in black smoker chimneys at the NW caldera vent field, Brothers Volcano, Kermadec Arc. *Geomicrobiology Journal* 26:552–569.

Templeton, A.S., E.J. Knowles, D.L. Eldridge, B.W. Arey, A.C. Dohnalkova, S.M. Webb, B.E. Bailey, B.M. Tebo, and H. Staudigel. 2009. A seafloor microbial biome hosted within incipient ferromanganese crusts. *Nature Geoscience* 2:872–876.

Wessel, P., D.T. Sandwell, and S.-S. Kim. 2010. The global seamount census. *Oceanography* 23(1):24–33.

Wheat, C.G., P. Fryer, K. Takai, and S. Hulme. 2010. Spotlight 9: South Chamarro Seamount. *Oceanography* 23(1):174–175.

Wheat, C.G., H.W. Jannasch, J.N. Plant, C.L. Moyer, F.J. Sansone, and G.M. McMurty. 2000. Continuous sampling of hydrothermal fluids from Loihi Seamount after the 1996 event. *Journal of Geophysical Research* 105:19,353–19,367.

Wheat, C.G., M.J. Mottl, A.T. Fisher, D. Kadko, E.E. Davis, and E. Baker. 2004. Heat flow through a basaltic outcrop on a sedimented young ridge flank. *Geochemistry, Geophysics, Geosystems* 5(12), Q12006, doi:10.1029/2004GC000700.

White, D.C., T.J. Phelps, and T.C. Onstott. 1998. What's up down there? *Current Opinion in Microbiology* 1:286–290.

Whitman, W.B., D.C. Coleman, and W.J. Wiebe. 1998. Prokaryotes: The unseen majority. *Proceedings of the National Academy of Scienc of the United States of America* 95:6,578–6,583